THE EFFECTS OF INBREEDING, CROSS-BREEDING, AND SELECTION UPON THE FERTILITY AND VARIABILITY OF DROSOPHILA.

By W. E. Castle, F. W. Carpenter, A. H. Clark, S. O. Mast,
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INTRODUCTION.

PHYSIOLOGICAL characters are inherited no less than morphological ones. In each case there doubtless is in the germ a structural basis on which the development of the peculiarity in question rests. In no instance as yet have we been able to identify beyond question the physical basis of any particular character, but a first step in that direction has been taken in the discovery of specific morphogenic substances in the animal egg and of specific differences among the chromosomes of the germinal nuclei in both sexes. While cytologists attack the problem of heredity from the side of the structure of the germ-cells, it is important that their labors be supplemented by a study of the heritable characters themselves, so that the mutual relations of characters and the modifications which they undergo from generation to generation may be better understood.

Among physiological characters which beyond question are heritable may be mentioned fertility, i. e. the capacity for reproduction. This varies among individuals and among races, as every experienced breeder knows, but the conditions upon which it depends are somewhat uncertain. In some cases external conditions are supposed to induce sterility, as, for example, abundant nutrition and lack of exercise, resulting in excessive vegetative growth without reproductive activity. In other cases inbreeding is assigned as a cause of sterility, or sterility may occur spontaneously without any assignable cause. The relation of inbreeding to sterility has been studied experimentally in mammals by Crampe ('83), Bos ('94), and Guaita ('98) ; and in birds by Fabre-Domengue ('98). They all find the relation to be a causal one, continuous inbreeding, as of brothers and sisters, resulting in decreased fertility, attended more or less commonly by lack of vigor, diminution in size, partial or complete sterility, and pathological malformations. It was our expectation that similar effects would be observed in the fly, Drosophila, when

inbred continuously. This indeed seemed to be the result of our earlier experiments, but more extended observations indicate that close-breeding is not necessarily attended by decreased fertility, in this animal, but that particular degrees of fertility are transmitted in certain families irrespective of the consanguinity of the parents.

MATERIAL AND METHODS.

The organism used in this experiment in close-breeding was *Drosophila ampelophila* Löw, a small dipterous insect known under various popular names such as "the little fruit fly, pomace fly, vinegar fly, wine fly, and pickled fruit fly." These appellations indicate the class of substances in which the insect breeds. During the autumn it will commonly be found in the vicinity of fermenting fruit and decaying vegetable material. It is especially attracted by over-ripe grapes in the process of vinous fermentation. Through breaks in the skin of such grapes it lays its eggs, the resulting larvae feeding on the pulp.

A brief sketch of the life history of Drosophila will show that it is a form well adapted for experiments on inbreeding. The life cycle is rapidly completed, making it easy to obtain a large number of generations in a comparatively short period. The flies can be kept breeding the year round at ordinary room temperature on various fruits, some of which can be readily obtained at any season.

The imagoes become sexually mature within thirty-nine hours after hatching. The female can lay eggs in about forty-eight hours after emergence. The time may be, however, somewhat longer, depending probably on the attractiveness of the material furnishing a place for oviposition. Fermenting and decaying fruit seem to stimulate the laying of the eggs. At the end of three or four days the larvae appear and eat voraciously. The duration of the larval state varies considerably, but under favorable circumstances it may be completed within three days and the pupal state assumed. The larvae commonly seek dry places for pupation, usually leaving the food substance and crawling up the side of the vessel in which they are contained. The duration of the pupal condition, again, varies considerably, but may be completed at the end of about three days.

Allowing thus for the egg, larval, and pupal stages about three days each, and two for the imago to lay eggs, it follows that the whole life cycle may be completed within eleven or twelve days. But the average length of this cycle, when the whole year with its varying conditions is

taken into account, would probably lie somewhere between fifteen and twenty days.

The normal sexual proportion in this species appears to be one very nearly approaching equality. Mr. Thomas Ordway states (in a manuscript report) that there seems to be a slight excess of males, but that perhaps the proportion would be somewhat changed if larger numbers than he worked with were taken into account. One can say, at least, that neither sex predominates in any marked degree.

It has been our intention in these experiments to keep external conditions as nearly uniform and as nearly optimal as possible, but to breed only from brothers and sisters through a series of generations. The breeding was at first carried on in small glass battery-jars about 8 cm. deep and 6 cm. wide, each covered with a square of window-glass; later, tumblers of similar dimensions were used, and were found more convenient because of the flaring top. The jars were kept on a table in the laboratory at ordinary room temperature.

A single pair of flies (brother and sister) was put in each breeding-jar, and was kept supplied with an abundance of food. This consisted during generations 1–12 of the A series of fermenting grapes, but in subsequent generations of the A series, as well as throughout all the other series, it consisted exclusively of banana, in which fermentation was started either by the addition of a little yeast or with a little juice taken from a stock-jar of fermenting banana.

To guard against the possible production of half-brothers and half-sisters through matings of the same female with two or more males, the following method of forming pairs was adopted and continued up to the year 1904–5.

Pupae of the same parentage were put together, a pair in each of a number of jars. When the imagoes emerged, if in any jar they proved to be of different sexes, they were left together; if of the same sex, the flies were rearranged so as to bring those of opposite sex together. Thus each female was ultimately placed in a jar with a single male and allowed to remain there during its entire subsequent life, which usually lasted three or four weeks. Most pairs under these circumstances produced an abundance of eggs within three to five days, and pupae were found about a week later attached to the sides or cover of the breeding-jar. These were removed and counted from day to day before they had an opportunity to emerge as imagoes, and the parents were left in the jar to continue breeding as long as possible.

Pairs which produced no young by the end of two or three weeks were

recorded as sterile, and in some cases each parent was then placed with a new mate to ascertain, if possible, in which of the two parents the sterility lay. In some cases one or other of the two was found to be fertile by a different mate, but in no case were both found to be fertile by new mates. This result indicates that the sterility observed is not relative, but absolute; for an animal which is sterile toward one mate is sterile toward *all* mates.

BRIEF HISTORY OF THE *A* SERIES.

The experiment which was begun first and has been continued longest constitutes what we shall call the *A* series (see Table I and Figure 1). During the first year of this experiment (1901–2), when it was carried on by F. W. Carpenter, no record was kept of the number of sterile pairs, or the total number of young produced by each pair (except in generation 6, Table I), attention being directed chiefly to the effects of the inbreeding on variability. But beginning with the thirteenth generation, when A. H. Clark took charge of the experiment, records as complete as possible were kept of the number of fertile pairs and the number of young produced by each pair. Whenever a female was accidentally killed or escaped from the breeding-jar (as sometimes happened when pupae were being removed) before she had had an opportunity to lay her full quota of eggs, her brood was not used in making up the average for the generation, though the pair to which she belonged was recorded as fertile.

From generation 13 to generation 24 inclusive, Sept. 1902–June, 1903, the experiment was in charge of A. H. Clark and showed results of a pretty uniform character. Between seventeen and eighteen per cent of the pairs formed were sterile. The average number of young produced by a fertile pair was about 39; the maximum number, 145.

As a control on the results given by the *A* series during this period, pairs were from time to time taken from a stock-jar established in the following way. In October, 1902, flies captured at three different localities several miles apart were placed in a large covered jar within which was a smaller open jar containing fermenting banana. The flies soon increased, forming a vigorous colony, which was given no further attention beyond the occasional addition of fresh food. Three pairs taken from this jar in the latter part of October, 1902, produced remarkably vigorous broods numbering respectively 529, 560, and 260 young, an average of 450 young to a brood. Two pairs taken from the same jar about five weeks later gave a similar result, the broods numbering 623 and 361 respectively.

TABLE I. HISTORY OF SERIES A.

Inbred Generation.	Average Number Young (Sterile Pairs not included).	Maximum Number of Young in a Brood.	Pairs Fertile.	Pairs Sterile.	When reared.	Observer.	
6	125	151	3	0	March (?) 1902	F. W. Carpenter.	
13	..	..	2	1	Sept.–Oct.	A. H. Clark.	
14	..	55	2	2	October	"	
15	44	115	8	1	November	"	
16	59	75	4	1	Nov.–Dec.	"	
17	28	40	3	2	Dec. 1902–Jan.	"	
18	21	38	13	2	January [1903	"	
19	26	63	11	3	February	"	
20	43	116	12	2	March	"	
21	32	54	9	1	March–Apr.	"	
22	88	145	6	2	Apr.–May	"	
23	33	61	5	0	May	"	
24	72	86	5	1	June	"	
25	..	..	8	0?	June–July	"	
26	101	121	8	3	July–Aug.	W. E. Castle.	
27	128	138	8	2	August	"	
28	95	119	12	4	Aug.–Sept.	"	
29	153	196	9	4	September	"	
30	101	125	4	3	September	"	
31	4	7	3	4	October	"	
32	62	127	3	2	Oct.–Nov.	"	
33	55	103	7	4	Nov.–Dec.	"	
34	32	125	11	1	Dec. 1903–Jan.	"	
35	29	59	14	1	January [1904	"	
36	45	118	12	0	Jan.–Feb.	"	
37	43	105	6	0	Feb.–March	"	
38	126	257	11	1	March	"	
39	106	225	8	1	March–Apr.	"	
40	123	192	7	0	April	"	
41	174	296	12	1	May	"	
42	158	187	7	3	May	"	(Allowed to interbreed.
43	63	81	10	2	June	"	
44	..	..	6	0	June–July	"	
45	..	..	6	0	July	"	
46	..	..	4	0	July	"	
47	..	..	4	0	August	"	
48	..	..	..	..	...	"	
49	..	..	..	..	....		
50	100	178	6	0	October	W. M. Barrows.	
51	187	210	4	0	November	"	
52	63	93	6	0	December	"	
53	249	372	7	0	January, 1905	"	
54	262	301	5	1*	Jan.–Feb.	"	
55	308	397	6	0	Feb.–March	"	
56	280	357	6	0	March	"	
57	242	292	6	0	April	"	
58	229	341	6	0	Apr.–May	"	
59	135	229	4	0	May	"	

* ♂ sterile.

A brood reared a month later (in January, 1903) contained 178 young, but was probably incomplete, since it was produced in a very small jar containing an insufficient amount of food, and the food was not renewed, as was the practice in ordinary cultures.

Four control pairs taken from the stock-jar about four months later, in May, 1903, produced broods numbering 174, 142, 79, and 157 respectively. These numbers are very low compared with those obtained from control pairs in the previous fall, but it should be observed that the numbers obtained from the A series during this same period (generation 23)
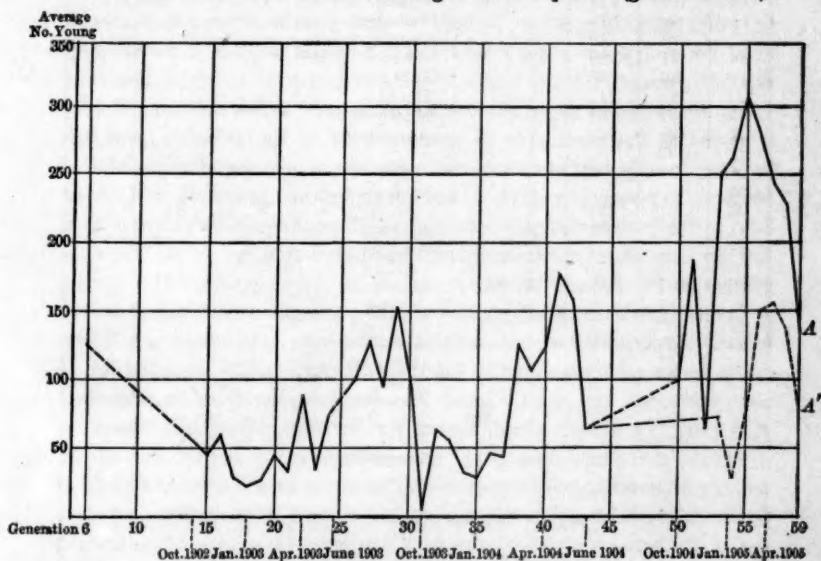
FIGURE 1. Productiveness of *fertile* pairs in the A series.

are likewise low. Very probably the falling off in both cases was due to low temperatures in the building, at about the time when the steam heat was discontinued, resulting in imperfect fermentation of the food, or directly affecting the egg production of the females. For the broods produced by the A series were larger both previous to this period and subsequent to it.

Broods of the control series were throughout this year several times as large as broods of the A *series reared simultaneously under identical conditions.* Further, no sterile pairs were encountered in the control series, though a considerable percentage of sterile pairs was constantly

found in the A series. The inference naturally drawn from these facts was that inbreeding had decreased the fertility of the A series, but subsequent investigations throw doubt on this conclusion.

The A series was continued from June, 1903, to October, 1904, by the senior author. The warm weather of the months June–September, 1903, gave the flies optimal conditions for reproduction, and naturally the average number of young in a brood rose somewhat, reaching its highest point in the 29th generation, 153.5 young to a brood. But throughout this period, notwithstanding the favorable conditions, a considerable proportion of the pairs proved sterile, amounting on the average to 28 per cent of the pairs formed. The average brood of a fertile pair was 124 young.

Ten control pairs from outdoor sources, kept under the same conditions and at the same time as generation 27 of the A series, were all fertile. In only four out of the ten cases was a full record made of the number of young produced. These four broods numbered 164, 204, 304, and 241 respectively, an average of 228 to a brood, which was just 100 greater than the average-sized brood produced by fertile pairs in generation 27 of the A series.

In October, 1903 (31st generation), the productiveness of the A series fell off sharply and the series seemed on the verge of extinction. Four out of seven pairs were sterile, and the three fertile pairs produced in all only twelve young. At the same time control pairs from outside were producing vigorous broods containing usually 200 or 300 individuals.

But in the subsequent (32d) generation, the A series seemed to recover its normal condition, and so continued for six generations (32–37), fertile pairs producing an average of 41 young. During this period 8 out of 59 pairs, or 13.5 per cent, were sterile.

For the next five generations (38–42) the productiveness of the A series was more than doubled. The rise occurred suddenly in generation 38, the parents for this generation having been mated in the last days of February. As this was by no means the most favorable season of the year, and the possibility of an accidental cross seems for a variety of reasons excluded, it is difficult to account for the sudden change, unless it is the expression of a cyclical variation in fertility. In this period 6 out of 51 pairs, or 11.7 per cent, were sterile, while the fertile pairs produced on the average 137 young. Two other series, M and N, started in the previous October, and kept under similar conditions, were at the same time producing between 200 and 300 young, or even more.

In generation 43 of the *A* series we have indications of the possible return of a period of depression. Ten fertile pairs produced on the average 62.8 young, the maximum number being 81. Two other pairs were sterile. During the next four generations (44–47, reared June–August, 1904), no record was kept of the number of young produced. Twenty pairs in all were used, all of which proved fertile. The young constituting the 47th generation emerged as imagoes about August 15, 1904, and contrary to previous usage were not separated, but were left in the jar where they had emerged, to mate freely *inter se*. About October 10, animals were withdrawn from the jar to start a new series of generations. In the meantime two generations had probably been produced, allowing of possible mating of cousins, rather than of brothers and sisters, as in all previous generations. See page 751 as to the effect of mating cousins.

On October 10, 1904, Mr. W. M. Barrows took charge of certain of the *A* jars, removing ten pairs from jar *A* 47.2 to form what we shall call generation 50. At least eight of the ten pairs were fertile, but they showed wide variation in the size of their broods, ranging from 12 to 239 young. The average size of the six complete broods, that is, broods reared in jars where the mother lived for at least three weeks, and in which the food was properly fermented, was 100. The average was higher still, viz. 187 in generation 51, but it fell to 63 in generation 52, probably as a result of low temperature. It rose again sharply in generation 53, following a transfer to a warm chamber, and continued to rise in the two following generations until an average of 308 was attained in generation 55. Following the attainment of this, for the *A* race, unprecedented maximum, there was a steady fall in the average to 135 in generation 59, where the experiments for the year came to an end.

A second branch of the *A* family (*A'*, Figure 1), taken from the miscellaneously bred descendants of jar *A* 47.3, ran a course nearly parallel with that of the branch already described, but attained a maximum average of only 156. The two were kept under identical conditions.

Low Productiveness Characteristic of the A Stock.

Looking back over the history of the *A* series for fifty-nine generations of almost continuous inbreeding (Figure 1), we see that the average number of young produced by fertile pairs had never been as high as 200 until the fifty-third generation (winter of 1905) ; usually it was under 100 ; and about 1 in 5 of the pairs formed had been sterile (at least in the period between the twelfth and forty-fourth generations). Control cultures

made under identical conditions, but from stock not inbred, had a productiveness two or three times as great and showed no signs of sterility. The A stock, accordingly, is characterized by low productiveness and an inclination to sterility. If these are effects of inbreeding, they began to show themselves early, the small productiveness as early as the sixth generation, the partial sterility as early at least as the thirteenth generation, and probably earlier. But it is very improbable that the low productiveness of race A was due to inbreeding, for when the inbreeding experiment was repeated with other stocks of flies no appreciable diminution of fertility occurred.

It cannot have been due to selection, conscious or unconscious, of parents from the least productive broods, for it was the practice of Messrs. Carpenter and Clark " to start a number of cultures and then breed from the one which succeeded best," which would be in general the *most* productive rather than the least productive pair. That selection is a very important factor, will presently appear. It certainly has a much greater influence on fertility than does inbreeding, so that selection from the most productive pairs is able to more than offset the effects of inbreeding. But it was not sufficient in the experiments of Carpenter and Clark to bring the A race up to normal productiveness. The low productiveness must have been present in the A stock at the beginning of our experiments and have persisted in spite of selection favoring increase of fertility.

Selections for High or Low Productiveness.

The bearing of selection from parental broods more or less productive upon the fertility of the race will be clear from Table II.

In the A series, between generation 30 and generation 43, pairs were several times taken simultaneously from parental broods of unequal size. The result is shown in Table II. The larger parental brood produces, as a rule, a larger average filial brood, and with a smaller proportion of sterile pairs. Thus, in the seven generations tabulated (which include all available data), if we weight each generation the same, the following average values are obtained from the lowest and highest parental broods respectively :

	Parental Brood.	Filial Brood.	Per cent Filial Pairs Sterile.
Lowest	96	91	23
Highest	185	104	13

TABLE II.

RESULT OF SELECTING PAIRS SIMULTANEOUSLY FROM BROODS OF DIFFERENT
SIZE BUT OF SIMILAR ANCESTRY IN SERIES *A*.

Generation.	Parental Broods.	Average Filial Brood, omitting Sterile Pairs.	Per cent Sterile Pairs.	Number of Filial Broods.
20	134	82	50	4
"	196	119	33	3
33	49	71	50	4
" *	127	53	33	6
35	25	25	14	7
"	50	29	0	3
"	70	20	0	3
"	128	43	0	3
39	145	90	20	5
"	257	127	0	4
40	87	165	0	3
"	225	110	0	3
41	79	161	0	3
"	161	163	17	6
"	192	195	0	4
43	154	46	25	4
"	167	80	25	4

* Two broods in this lot higher than any in foregoing.

This summary shows an unmistakable tendency for the larger parental brood to produce larger filial broods, but *not so much larger* as the difference in the parental broods would lead us to expect. In other words, there occurs *regression toward low productiveness*, which is a fixed racial

character of series *A*, or was in the period under discussion. Further
evidence as to the effects of selection on fertility, based on series *M* and
N, will be found on page 769.
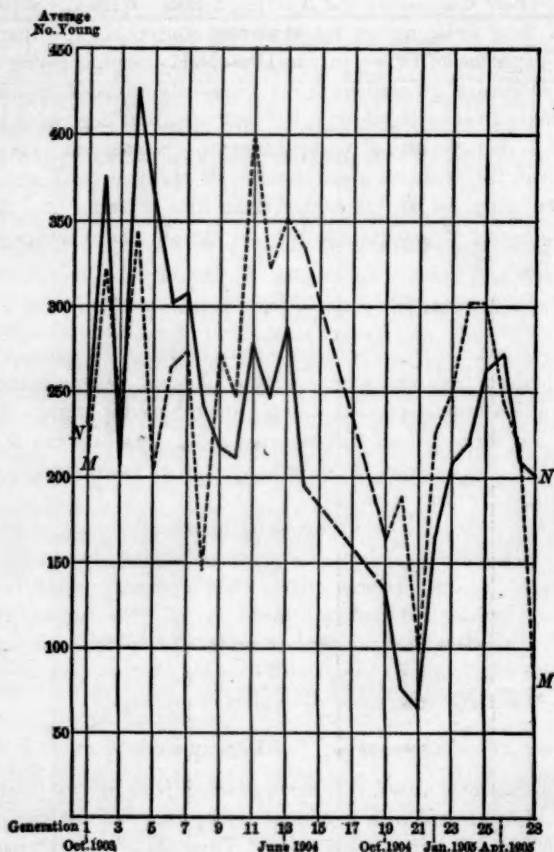

FIGURE 2. Productiveness of *fertile* pairs in the *M* and *N* series.

THE *M* AND *N* SERIES.

Two other inbred series, *M* and *N* (Tables VIII and IX, and Figure
2), started by S. O. Mast, showed during the first fourteen inbred gener-
ations productiveness much higher than that of series *A*. The average
never fell below 200, except in a single generation of each series, and

was usually nearer 300, occasionally rising to 400 or even higher. The *M* series shows a few sporadic cases of sterility; the *N* series, none whatever. The *M* series shows on the whole a rise of the average during the period under discussion; the *N* series, a fall. With the subsequent history of these series we are not at present concerned. Comparison of the three experiments shows, that in Drosophila close inbreeding during fourteen successive generations is not necessarily attended by either decreased productiveness or sterility, but that particular degrees of productiveness are characteristic of particular races. Subsequent experiments indicate that the productiveness of series *M* and that of *N*, during this period, are much nearer the normal than that of series *A*. A more complete account of generations 1–14 of the *M* and *N* series will be found on page 757.

Other Families of Drosophila.

In the summer of 1903 observations were made on the productiveness of flies obtained from two other sources. A stock, *D*, was reared from eggs found in a banana purchased in a Cambridge fruit store. Another stock, *F*, was formed from flies captured about a garbage can at a distance of half a mile from the laboratory, and at more than a quarter of a mile from the fruit store.

Four pairs from the *D* stock produced broods numbering respectively 164, 204, 304, and 241 young, the average number being 228. Six pairs from the *F* stock produced broods which were only in part recorded. The smallest number credited to a brood was 85; the largest, 220. It is probable, therefore, that the productiveness of this stock was similar to that of stock *D*, though perhaps a little lower. Both stocks, *D* and *F*, resemble *M* and *N*, rather than *A*, in productiveness.

Effects of Cross-breeding.

The question now arises, if a stock characterized by low productiveness, like *A*, is crossed with a normal stock, what will be the productiveness of the offspring? Further, if Drosophila is indifferent to a considerable amount of inbreeding, will it be indifferent also to crossbreeding? To throw light on these questions, a number of crosses with the *A* stock have been made at various times.

Experiments of A. H. Clark.

In March, 1903, when the *A* series was producing an average of 43½ young to a pair, two females from the *A* stock were mated with males

from the stock-jar mentioned on page 735. Their broods of offspring numbered 43 and 24 respectively, but the latter may have been incomplete, as the mother died within fourteen days after the culture was started. At any rate, there was no indication of any increased productiveness by *A* females on account of their being mated with males from a different stock. Two pairs, representing a cross reciprocal to the foregoing (*i. e.*, ♀ from stock-jar × ♂ *A*), produced broods numbering 91 and 132 respectively, i. e. two or three times as many young as the first mentioned crosses yielded. As this was about the usual relation of broods of normal series to those of the *A* series, it seems that the productiveness of the female is unaffected by the productiveness of the race to which her mate belongs. Subsequent experiments support this idea. But whether the *offspring* of a female would be affected in productiveness by the cross is an entirely different question. A single experiment was made at that time which bears on this matter. A pair taken from the 132 young produced by the cross, ♀ from stock-jar × ♂ *A*, yielded, in April, 1903, 116 young. The *A* series produced at this time an average of 32.4 young to a brood. The productiveness of the daughter was in this case similar to that of her mother, rather than that of the *A* race from which the father came.

Experiments of W. E. Castle.

More extensive experiments in crossing the *A* stock were made in July and August, 1903, parallel with generation 27 of the *A* series, which, it should be remembered, produced an average of 128 young to a brood, under the favorable summer conditions.

CROSS 1. $A ♀ × D ♂$.		CROSS 1a. $D ♀ × A ♂$.	
Pair 1 . . .	sterile.	Pair 1 . . .	sterile.
Pair 2 . . .	146 young.	Pair 2 . . .	337 young.
Pair 3 . . .	106 "	Pair 3 . . .	315 "
Pair 4 . . .	150 "	Pair 4 . . .	206 "
Pair 5 . . .	114 "	Pair 5 . . .	163 "
Av. for fertile pairs, 129 young.		Av. for fertile pairs, 255 young.	

In Crosses 1 and 1a, as in the previously described experiment, females of each race apparently had their productiveness unaffected by the cross-mating; for *A* females produced an average of 129 young by *D* mates, and 128 young by *A* mates. Exactly one pair in five is fruitless in each sort of mating. On the other hand, *D* females pro-

duced 255 young by A mates, and 228 young by D mates (see page 743). The sterility of Pair 1 in Cross 1a was probably inherent in the A male, as will subsequently appear.

Cross 2. $A\,♀ \times F\,♂$.		Cross 2a. $F\,♀ \times A\,♂$.	
Pair 1 . . .	142 young.	Pair 1 . . .	189 young.
Pair 2 . . .	162 "	Pair 2 . . .	189 "
Pair 3. . . .	176 "	Pair 3 . . .	186 "
Pair 4 . . .	165 "	Pair 4 . . .	283 "
Average, 161 young.		Average, 212 young.	

The A females employed in Cross 2 seem to have been more productive than those employed in Cross 1. Further, the F females of Cross 2a were less productive than the D females employed in Cross 1a. Accordingly the averages for the reciprocal crosses, 2 and 2a, are not so unlike as are those for Crosses 1 and 1a. Nevertheless, in one case as in the other, the A females are much the less productive.

Cross 3. $A\,♀ \times$ stock-jar $♂$ (p. 735).			
Pair 1 . . .	129 young.	Pair 5 . . .	88 young.
Pair 2 . . .	115 "	Pair 6 . . .	126 "
Pair 3 . . .	150 "	Pair 7 . . .	113 "
Pair 4 . . .	156 "		
	Average, 125 young.		

In a third cross (Cross 3), the reciprocal of which was not performed, A females were mated with males from the stock-jar (p. 735). They showed about the same productiveness (125) in this case as when mated with their own brothers (128), or with D males (129, Cross 1).

A control cross (Cross 4), made at the same time as the foregoing, between F females and D males, produced an average of 219 young, which agrees closely with the average, 212, produced by F females when mated with A males (Cross 2a).

Cross 4. $F\,♀ \times D\,♂$.	
Pair 1	199 young.
Pair 2	256 "
Pair 3	263 "
Pair 4	159 "
Average, 219 young.	

These several experiments agree in showing that the fecundity of a female is unaffected by the relatedness or unrelatedness of her mate. In other words, the racial fecundity of the male in no case affects the productiveness of his mate, unless he is a wholly sterile animal.

Certain of the young produced by Cross 1, Pair 2, were bred *inter se.* Of ten pairs tested, all were fertile, though the record for one was incomplete on account of an accident. The average number of young produced by the remaining nine pairs was 356. The broods produced by the ten pairs individually were as follows:

Pair.	Young.	Pair.	Young.
G 7.1 . . .	[44] (incomplete)	G 7.6 . . .	393
G 7.2 . . .	338	G 7.7 . . .	412
G 7.3 . . .	408	G 7.8 . . .	388
G 7.4 . . .	339	G 7.9 . . .	269
G 7.5 . . .	359	G 7.10 . . .	297

Average, 356 young.

This is a remarkably high average. The *A* race at this same time (generation 28), and under identical conditions, was producing an average of 95 young to a pair; and pure *D* pairs in the previous generation had produced an average of 228 young, while pure *D* females mated with *A* males had produced 255 young, 100 less than the average brood of their cross-bred offspring.

Young from the reciprocal cross, 1*a*, Pair 5, were likewise mated *inter se.* Eight pairs were tested, all fertile. Their broods were as follows:

Pair.	Young.	Pair.	Young.
G 18.1 . . .	283	G 18.5 . . .	[66] incomplete.
G 18.2 . . .	335	G 18.6 . . .	[178] "
G 18.3 . . .	316	G 18.7 . . .	173
G 18.4 . . .	227	G 18.8 . . .	180

Average, 252 young.

The average number of young, 252, is not much greater than the general average for Cross 1*a*, though the particular brood (Pair 5, Cross 1*a*) from which the parents were derived contained only 163 young, and the average for pure *D* pairs had previously been found to be 228. On the whole, therefore, this cross, like the reciprocal one previously discussed, seems to have increased the productiveness of the cross-bred offspring, making it greater than that of either parent race when purely mated or when cross-mated.

Experiments of S. O. Mast.

The experiments of Mr. Mast, made at various times between November, 1903, and May, 1904, support this conclusion in part.   Mr. Mast made crosses (5, 5a, 6, and 6a) between flies from generations 31–40 of the A series (which was then producing about 50 young to a pair), and mates taken from two new series, M and N, which commonly produced 200–400 offspring to a pair, or even more (see Figure 2, p. 742, and Tables VIII and IX, pp. 758, 759).

CROSS 5. A ♀ × M ♂.

Pair 1 . . . 42 young.
Pair 2 . . . 79 "
Pair 3 . . .   6 "
Average, 42 young.

CROSS 5a. M ♀ × A ♂.

Pair 1 . . . 365 young
Pair 2 . . . 379 "
Pair 3 . . . 597 "
Average, 447 young.

CROSS 6. A ♀ × N ♂.

Pair 1 . . . 11 young.
Pair 2 . . . 55 "
Pair 3 . . . 25 "
Pair 4 . . . 22 "
Pair 5 . . . 32 "
Pair 6 . . . 28 "
Pair 7 . . . 84 "
Pair 8 . . . sterile
Pair 9 . . . 15 "
Pair 10 . . . 36 "
Pair 11 . . . sterile
Pair 12 . . . 95 "
Pair 13 . . . 90 "
Av. for fertile pairs, 45 young.

CROSS 6a. N ♀ × A ♂.

Pair 1 . . . 234 young.
Pair 2 . . . 435   "
Pair 3 . . . 299   "
Pair 4 . . . 279   "
Pair 5 . . . 209   "
Pair 6 . . . 187   "
Pair 7 . . . [186] "
incomplete.

Av. for pairs 1–6, 274 young.

Mr. Mast also mated females of A 36 (average young to a pair, 45) with males taken from a stock-jar started a short time previously with normal individuals similar to the M and N series.   This will be called Cross 7.   The reciprocal cross was not made.

CROSS 7. A ♀ × stock-jar ♂.

Pair 1 . . .   33 young.
Pair 2 . . . 132 "
Pair 3 . . .   22 "
Average, 62 young.

The three crosses, 5, 6, and 7, show a result entirely normal for the *A* series; and the reciprocal crosses, 5*a* and 6*a*, show a result normal for the *M* and *N* series.   In each case the productiveness of the mother is unaffected by the character of her mate, precisely as in crosses 1–4, and their reciprocals.   Pairs of cross-bred individuals produced by crosses 5–7, when mated brother with sister, showed a marked increase in productiveness as compared with that of their respective inbred mothers.

	Average Mother's Brood.	Average Daughter's Brood.
Cross 5	42	187 (omitting three sterile pairs).
Cross 6	45	229
Cross 7	62	275

In the crosses reciprocal to 5 and 6, viz. 5*a* and 6*a*, the mothers came from races unusually fertile and not extensively inbred; no increase of fertility was observable among their offspring as a result of a cross with the *A* series.

	Average Mother's Brood.	Average Daughter's Brood.
Cross 5 *a*	447	353
Cross 6 *a*	274	274

The cross-breds, like their mothers, showed a high productiveness. This was probably neither increased nor diminished materially by the cross with the unproductive *A* race.   The apparent falling off on the part of the young produced by Cross 5*a*, from 447, the average mother's brood, to 353, the average daughter's brood, is due to the unusual size of the maternal average.   This in turn was due to the occurrence of a single very large brood, 597, in Cross 5*a*, the other broods numbering 369 and 379 respectively, which is not very different from the average daughter's brood, 353.   While the cross-breds from Cross 5*a* were producing broods of this size, the uncrossed *M* race was producing broods averaging 273.   While the cross-breds from Cross 6*a* were producing broods averaging 274 in number, the uncrossed *N* race produced a single complete brood of 277 young.   We conclude that in the early generations of the *M* series and up to the ninth generation at least of the *N* series, the inbreeding had not materially affected the productiveness of those races, for, among other reasons, a cross with an unrelated and more extensively inbred race (*A*) did not affect the productiveness of the cross-breds, which remained normal, like that of the pure *M* or *N* races respectively.

Mr. Mast's subsequent experiments, however, show that the unproductive A race did show its influence in the second cross-bred generation (generation F_2), so that the cross did not eliminate wholly the unproductiveness inherent in the A race. For sterility and low productiveness reappeared after skipping a generation, in certain of the grandchildren, as will be shown by an examination of Tables X–XIV. This occurred in two out of five families, following a cross between a normal female and an A male. This observation shows that an entirely fertile male may transmit partial or complete sterility of the female sex as a racial character to his grand-daughters, though not apparently to his daughters.

The reciprocal cross, A ♀ × normal ♂ (Tables XV–XVIII), resulted in one case in the production of females half of which were sterile (Table XV), the other half being of low productiveness. This case shows that a female of a race inclined to sterility may transmit that character *directly* to her cross-bred offspring (generation F_1). The males of race A in Mr. Mast's experiments transmitted sterility to the grand-daughters only, never to the daughters. This difference in heredity through the two sexes would seem to indicate that sterility of the female is dependent upon egg structure rather than sperm structure, the eggs produced by mothers of a fertile race always yielding fertile daughters. But the eggs of cross-bred females, whose father was of an infertile race, produce some of them fertile, some infertile females.

Experiments of W. M. Barrows.

Though the M and N races, after nine or fewer generations of inbreeding, were not rendered more productive by a cross with race A, such was not the case after an additional year of inbreeding. In March, 1905, Mr. Barrows made crosses between the M and N races (then inbred for twenty-four generations), and between each of these and the A race (then inbred for fifty-four generations). See Tables III–V. The cross-mated mothers in each case gave a normal result (F_1), without any increased productiveness on account of the unrelatedness of their mates. But their cross-bred offspring, with equal regularity, showed increased productiveness (F_2), which surpassed that of either parent race under the same conditions.

At the same time Mr. Barrows made crosses between two sub-families of the A race (A and A'), which had arisen from a common ancestry some eleven generations previously. See Figure 1, A and A', and Table VI. The two cross-mated mothers had broods considerably smaller than their sub-family (A') was at the time producing, but their cross-bred

daughters showed a productiveness just about equal to that of the A' sub-family under the same conditions. The average brood of the cross-bred mothers was 237, that of the purely mated A' mothers was 242.

TABLE III.

EFFECT OF CROSSING RACES M AND N, EACH INBRED FOR TWENTY-FOUR GENERATIONS.

Generation.	Uncrossed M Race, Average Brood.	Uncrossed N Race, Average Brood.	$M \times N$ Cross-breds, Average Brood.	Number of Cross-bred Pairs.
24	302	220		
25	302	262	$291 = F_1$	5
26	244	272	$341 = F_2$	

TABLE IV.

EFFECT OF CROSSING RACES A AND M, INBRED FOR FIFTY-FIVE AND TWENTY-FOUR GENERATIONS RESPECTIVELY.

Generations.	Uncrossed A Race.	Uncrossed M Race.	$A \times M$ Cross-breds.	Number of Cross-bred Pairs.
55, 24	308	302		
56, 25	280	302	$212 = F_1$	2
57, 26	242	244	$341 = F_2$	

TABLE V.

EFFECT OF CROSSING RACES A AND N, INBRED FOR FIFTY-FIVE AND TWENTY-FOUR GENERATIONS RESPECTIVELY.

Generations.	Uncrossed A Race.	Uncrossed N Race.	$A \times N$ Cross-breds.	Number of Cross-bred Pairs.
55, 24	308	220		
56, 25	280	262	$235 = F_1$	3
57, 26	242	272	$298 = F_2$	.

TABLE VI.

EFFECT OF A CROSS BETWEEN TWO DIFFERENT LINES (A AND A')
OF THE SAME INBRED STOCK.

Generation.	Uncrossed A Race.	Uncrossed A' Race.	$A \times A'$ Cross-breds.	Number of Cross-bred Pairs.
55	308	75		
56	280	150	$117 = F_1$	2
57	242	156	$237 = F_2$	

Accordingly it appears that separation for eleven generations had not made the two sub-families of the A race sufficiently unlike to profit by a cross between them. The cross-breds were no more productive than the more productive parental sub-family.

But any two *unrelated* inbred families are clearly mutually benefited by a cross between them. Their offspring are more productive than either parental race (Tables III–V).

Matings of Cousins not more Fruitful than those of Brother and Sister.

That a mating between cousins of an inbred race is not more fruitful than a mating between brother and sister of the same race has been shown by experiments among which only the following need be mentioned. Twelve matings were made between cousins in generation 28 of the A series. Three of these were sterile and two others produced incomplete broods of young. The average brood of the remaining seven pairs was 105. The uncrossed A race, generation 29, reared under identical conditions, consisted of four sterile pairs and nine fertile ones. The latter produced broods averaging 153 in number. Further, the young of the cousins bred *inter se* gave the following result. Four out of fourteen pairs were sterile, the remaining ten produced an average of 112 young. The uncrossed A race, generation 30, reared simultaneously and under identical conditions, gave broods averaging 101, produced by five fertile pairs, three pairs being sterile.

CYCLICAL VARIATIONS IN FERTILITY AND THEIR RELATION TO EXTERNAL CONDITIONS AND TO INBREEDING.

One of the most striking features of the record of the A series is the cyclical rise and fall of the productiveness. (See Figure 1.) This was

already low in generation 6, and kept on declining until, in January, 1903 (generation 18), the average had sunk to 21. From this point on a gradual rise followed, which ended abruptly in generation 29 (September, 1903). Then the productiveness fell off until, in January, 1904, the average brood numbered 29 young. Again it began to rise, as it had done the previous year. The rise was more rapid than in 1903, and reached a point somewhat higher. It also culminated (generation 41) sooner (in May rather than in September), and then began to decline again. In the fall of 1904 the productiveness of the *A* series was just about what it had been the previous spring, but showed a tendency to decline. Early in January, about the time recovery had begun in the two previous years, the cultures of the *A* series, together with those of series *M* and *N*, were transferred to a warm chamber. A remarkable increase in productiveness followed, which culminated in March (generation 55). The *A* broods then averaged 308 to a pair, but from that time on they steadily diminished in size, until at the end of May they had fallen to 135.

Each year the *A* series showed a gradual rise of productiveness followed by an abrupt decline. The annual rise follows a depression which occurs under fall conditions, in which low temperature is doubtless an important factor. Out of doors the rise would doubtless come in the spring, but in the warm laboratory it sets in earlier and culminates earlier. The culmination occurs in the three successive years in September, in May, and in March respectively. Each year the *A* series reached a higher maximum, until one branch of it at least seems to have become fully normal in productiveness, though another branch (*A'*, Figure 1) had still about the same productiveness in 1904-5 as in the previous year.

The *M* and *N* series (Figure 2) during the first nine months of inbreeding (generations 1-14) showed no marked change in productiveness. The *M* series showed on the whole a rise, the *N* series a fall, in productiveness. Both were evidently influenced by the same set of external conditions because the *M* and *N* curves generally show corresponding elevations and depressions. The *N* cultures were on the whole more vigorous; they showed no sterility whatever, whereas sterility did occur sporadically in the *M* series. Nevertheless the *N* series was apparently declining in fertility (perhaps because it had been *above* the normal in fecundity), while *M* was rising. In the second year of inbreeding (generations 19-28) both the *M* and the *N* series were less productive than in the previous year. The reverse was true of the *A* series in the

same two seasons. Hence it seems not improbable that inbreeding was causing a decline of fertility in series M and N, while series A under continuous inbreeding was gradually recovering its lost fertility.

But it is not certain that the change in productiveness of M and of N was due to inbreeding ; it may have been due wholly to changed conditions. The cultures of the two years were made by different persons, and their methods may have been different enough to account for the difference in results.

There can be no doubt, however, that a change had occurred in series A, which was now twice as productive as it had been the previous year, equalling the M and even surpassing the N series. This result was so surprising that as soon as it became fully evident, a second line (A') of the A series was started, drawn from a different culture jar. This showed a productiveness similar to that of the A series the previous year. (See Figure 1, A and A'.) Accordingly there would seem to have occurred a marked increase of fertility in one jar of the A series, but not in another.

When the cultures were transferred to a warm chamber in January, 1905, M and A responded promptly by a sharp rise in productiveness. Their

FIGURE 3. Synchronous cultures of 1904-05.

courses through the next five months were closely parallel (see Figure 3). Series N and A' responded in a similar way, but without attaining so high an average productiveness, series N because of a selection of broods of low productiveness (see page 756), series A' because of inherited low productiveness.

In the year 1904-5 two independent lines were maintained by Mr. Barrows in each of the series A, M, and N. The record of each of these

lines is shown separately in Figure 4, A and A'', M and M', N and N'. The two lines of each series pass through similar cycles, though not quite synchronously; yet the two lines of each series were reared synchronously. Thus, A reaches a maximum two generations (six or eight weeks) later than A''; M culminates a generation later than M'; and N' culminates four generations later than N. The last case is particularly interesting because in this series alone of the three the attempt was made to select
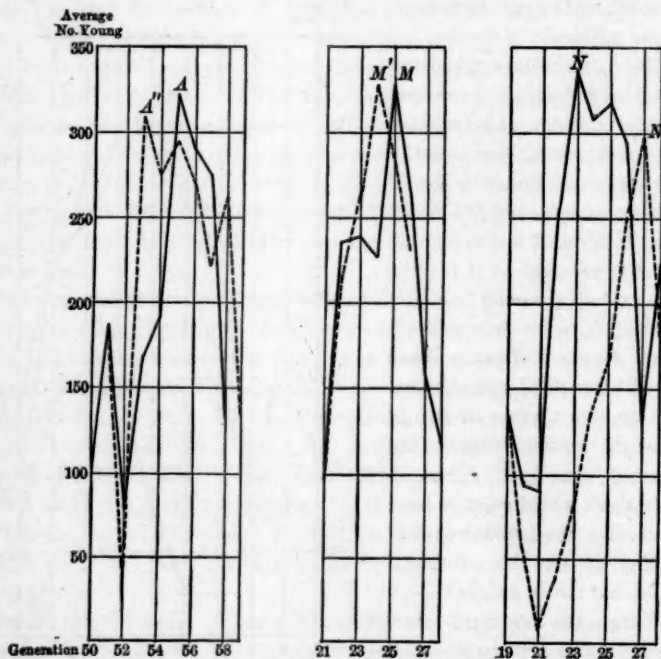
FIGURE 4. Productiveness of the two lines maintained in 1904–1905 in each of the three races, A, M, and N.

pairs from the most productive and the least productive broods respectively in the two lines. To carry out the selection proved in practice a difficult matter, because one cannot tell in the early stages of the cultures which brood will prove to be largest, so that he must either breed from all the cultures or else use the imagoes which emerge late. To do the former is very laborious, and the latter is undesirable because the late hatched individuals may be under normal size owing to deficient or too sour food.

The character of the selections made is shown in detail in Table VII, but may be summarized thus:

TABLE VII.

GENEALOGY OF N SERIES, 1904–5 (W. M. BARROWS).

Generation.	Av. Young, N Line.	N.			N'.			Av. Young, N' Line.
19			104			189		
20	93	77	113	90	43	61	70	58
21	90	86	95	St.	Fertile		10	10?
22	256	214		299	67		11	39
23	336	305	347	355	67	105	74	82
24	308	290	336	297	129	116	157	134
25	317	376	259	Fertile	159	257	81	166
26	295	233	400	252	265	238	245	249
27	131	11	205	178	321	326	219	289
28	221	198	251	213	201	174	167	181

There were usually three broods to choose from in each line, which we may call the largest, the medium-sized, and the smallest, respectively. In each line pairs were as a rule taken from one brood only. The broods selected were as follows:

	Largest.	Medium.	Smallest.
In the N line	5	1	3
In the N' line	4	2	3

The character of the successive choices in each line was as follows, L standing for largest, M for medium, and S for smallest:

Generation	19	20	21	22	23	24	25	26	27
N line	S	M	S	L	L	L	S	L	L
N' line	L	S	S?	S	L	S	L	S	L

The so-called smallest broods of the N line were larger than the largest broods of the N' line in generations 21 and 25, so that the choices of " smallest " broods in the N line do not mean much. They were not intended as choices of small broods, and in fact those chosen were not small broods, though they happened to be *less* large than the two other broods of the same line.

The broods selected as smallest in the N' line were in most cases really small. The choices of smallest broods coming in succession, in generations 20, 21, and 22 respectively, seem to have given the N' line a character of low productiveness, from which, however, it steadily recovered when medium or largest broods were selected. No doubt if the selection of small broods had been consistently followed up in generations 23–27, the N' line would have continued lower in productiveness than the N line, just as the A' line continued lower than the A line (Figure 1), though reared under identical conditions and without conscious selection of broods.

These experiments make it clear that Drosophila is in fecundity much influenced by external conditions, such as temperature, upon which is dependent the proper fermentation of its food. This is strikingly shown also in Figure 3. But independently of external conditions some families are characterized by high productiveness, others by low. Improved conditions increase the productiveness of all, by starting them on a cycle of greater productiveness. But the response is more prompt and vigorous on the part of a race normally high in productiveness. Long continued inbreeding may possibly cause a decline in the fertility of Drosophila (for cross-breeding two inbred stocks certainly causes a rise in fertility of the offspring), but the influence of inbreeding on fertility is less than variations in fecundity due to other causes, so that selection of the more fecund broods would certainly maintain a normal fertility even under the closest inbreeding for fifty or more generations.

FURTHER DETAILS CONCERNING EXPERIMENTS OF S. O. MAST.

Crosses were made between a stock of flies (series A) inbred for over thirty generations, and two other stocks (series M and N) inbred for from one to nine generations.

History of the M and N Series.

The M and N series were descended from two pairs (M and N) captured on decaying apples in an orchard three miles north of Cambridge, October 1, 1903. Their progeny were inbred (brother with sister) as a control on the results of the A series obtained in previous years, and also to obtain a stock of known productiveness to use in crosses with the A series.

In Tables VIII and IX are shown the line of descent and the size of broods of flies, each produced by a pair (brother and sister) descended from one of the original pairs M and N, which were captured on decaying apples as already stated. The successive generations are designated M and N respectively, followed by a numeral to indicate the number of generations of inbreeding which had occurred in its production.

No sterile individuals were found in the N series, while in the M series one sterile female was found in the seventh generation, another in the tenth, and a sterile male in the fourteenth. A second male, probably sterile, was encountered in generation 5. In the three cases of sterility first mentioned, the suspected individuals were proved to be sterile by subsequently mating them with individuals that were known to be fertile. The second matings, like the original ones, proved unfruitful.

In the M series, the average brood in the first inbred generation was 213, while the average for the series as a whole is 280, an apparent increase of fertility under close breeding. In the N series, generation 1 gave an average of 231 young, while the series as a whole gave 278.5 young to a brood. But the first inbred generation may have been lower than the average because of less perfect methods of treatment. If we divide the series into first and second halves, we find that series M is more productive in the second half than in the first, while the reverse is true of N. The average brood is in:

	Generations 1-7.	Generations 8-14.
M series	263	296
N series	317	240

TABLE VIII. GENEALOGY OF *M* SERIES (1903-4).

Pair *M.*

[Number of young?] Brother × Sister

Generation.					Average No. Young.
1	241	313	166	204	213
2	363	375	335	210	321
3	109			338	223
4	396			290	343
5	? ♂ sterile			205	205
6	228		237	327	264
7	♀ sterile		234	313	273
8	189		182	67	146
9	247		265	303	272
10	262		234	♀ sterile	248
11	351		385	460	399
12	332			315	323
13	454	341	281	335	352
14	335			♂ sterile	335

Average for series . . . 280

TABLE IX. GENEALOGY OF *N* SERIES.

Pair *N*.

[Number of Young?] Brother × Sister.

Generation.					Average No. Young.
1	241	313	166	204	231
2	375			377	376
3	273			142	207
4	397			459	428
5	367			[32?]	367
6	233		332	343	302
7	346		274	305	308
8	167		280	280	242
9	189		236	233	219
10	269	[25]	107	258	211
11	277		[141]	[90]	277
12	290			204	247
13	288		226	353	289
14	171	[89]	183	232	195

Average for series . . . 278.5

TABLE X.

GENEALOGY OF *M A* SERIES.

(Cross 5a, page 747; see also Table XI.)

$$M\,1\,♀ \times A\,32.5\,♂$$
$$[241] \quad [9]$$

	Synchronous Broods, A Series.	Synchronous Broods, M Series.	Average No. Young.
	55	321	372
	32	228	358 (Av. 373)
			229
			324
			609
			332
	29	343	240
			275 (Av. 294)
			253
			238
			291
	45	205	253

379
365
200 (Av. 334)
293
509
St. 237
St. 23
St. 226
St. 112
252
105
264 (Av. 181)
272
401
361
294
189
268
272
421
326
280
235
290
144

Generation.

MA 1

MA 2

MA 3

MA 4
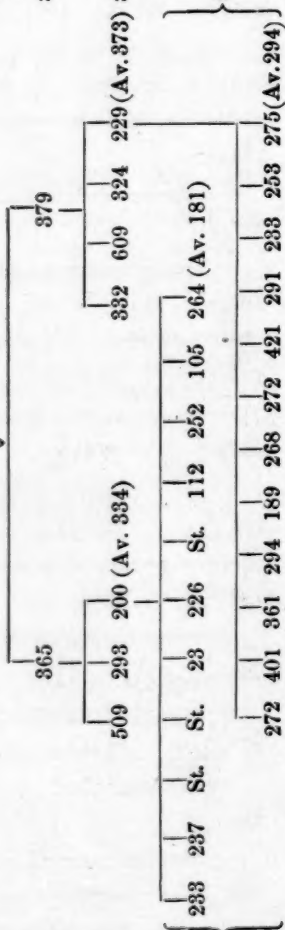
Dividing the series as nearly as possible into three periods of equal length, we obtain a similar result, as follows:

	Generations 1-5.	Generations 6-9.	Generations 10-14.
M series	261	239	331
N series	322	268	244

Series M is more productive in the last five than in the first five generations, while the reverse is true of N. Since the changes in the two series are opposite in nature it is improbable that they are due to inbreeding.

Crosses of Series M and N with Series A.

In Tables X–XVII are shown the results of crosses of the M and the N series with the long inbred A series. The cross-bred offspring were usually mated *inter se* (brother with sister) for one or more generations to observe the effects of the cross upon the subsequent history of the race. The generations of cross-breds are designated by the names of the two parental series, the maternal always coming first, followed by a numeral indicating the number of generations which have elapsed since the cross was made. Thus the offspring of the cross, $M ♀ × A ♂$, are designated $MA1$, their children $MA2$, and their grandchildren $MA3$. The offspring of the reciprocal cross, $A ♀ × M ♂$, are $AM1$, their children and grandchildren $AM2$ and $AM3$ respectively.

The size of the broods, from which came the individuals used in making a cross, is indicated by numerals in brackets placed below the designation of the parental brood.

TABLE XI.

GENEALOGY OF MA SERIES.

(Cross 5a, page 745; see also Table X.)

Generation.		Average No. Young.	Synchronous Broods, M Series.	Synchronous Broods, A Series.
	M 2 ♀ × A 31.5 ♂ [321] [7]			
MA 1	597		223	62
MA 2	279 304 223 498 434	**346**	343	55
MA 3	96 229 230 Fertile 488 Fertile 497	**361**	205	32

TABLE XII.

GENEALOGY OF NA SERIES.

(Cross 6a, page 747; see also Tables XIII and XIV.)

Generation.		Synchronous Broods, A Series.	Synchronous Broods, N Series.	Average No. Young.
NA 1	St. 29 216 5 321 22 20 178 6 65 190 208 211 141 138	55	376	334
NA 2	$N1\,♀ \times A\,30.2\,♂$ [318] [67] 234 435	32	207	?
NA 3	[100] [187] incomplete	29	428	125
NA 4	286 207 265 322 171 193	45	367	241

An examination of these tables shows:

(1) That a female of the A series mated with a male of series M or N does not have her productiveness increased thereby. See Tables XV, XVI, XVII, and XVIII.

(2) That a female of series M or N mated with a male of the A series does not have her productiveness diminished thereby. See Tables X, XI, XII, XIII, and XIV. The reverse seems to be true in certain cases, but this was probably due to the bestowal of special care upon the cross-mated series. In the case of those recorded in Tables XI and XIII this is almost certainly true ; the jars of cross-mated flies were in those two instances transferred to a room warmer than that in which the pure M and N series were reared.

TABLE XIII.

GENEALOGY OF NA SERIES.

(Cross 6a, page 747; see also Tables XII and XIV.)

Generation.	$N\,2\;\female \times A\,31.5\;\male$ [376] [7]						Average No. Young.	Synchronous Broods, N Series.	Synchronous Broods, A Series.
NA 1			435					207	62
NA 2	388	352	581	421	464	375	430	428	55
NA 3	Fertile	243	307	272	Fertile		274	367	32

It follows from (1) and (2) that low productiveness in Drosophila is due to low productiveness of eggs, not of spermatozoa. Complete sterility, however, may be found in either sex, as is shown by the history of both the A and the M series.

(3) The daughters of an A female by an M or an N male produce more young than their mother did, and more than other A mothers do under identical conditions. Their productiveness does not differ materially from that of purely mated M and N mothers, though *complete* sterility may appear among them.

(4) The daughters of an M or an N mother by an A male are on the whole similar in productiveness to their mother and to purely mated M and N mothers. None of the daughters has been found sterile.

TABLE XIV.

GENEALOGY OF NA SERIES.

(Cross 6a, page 747; see also Tables XII and XIII.)

$N \, \text{\textcurrency} \times A \; 40.4 \, \text{♂}$

	Synchronous Broods, A Series.	Synchronous Broods, N Series.	Average No. Young.
	174	211	243
	158	277	341
	68	247	272

[236]

[79]

$NA 1$

299   279   209   187   [186]

328   219   277   339   251 (Av. 283)

$NA 2$

482   318   318   390   411   [67] (Av. 399)

384   511   254   217   315   292   268   227   281   236   328   187   131   240 (Av. 289)

233   243 (Av. 304)

$NA 3$

Generation.

(5) The grandchildren produced by either of the reciprocal crosses between the A series and the M or N series vary much in productiveness. Some are sterile or of low productiveness like mothers of the pure A race. These occur oftenest among the young of cross-bred pairs of low

TABLE XV.

GENEALOGY OF $A M$ SERIES.

(Cross 5, page 747.)

Generation.	A 36.17 ♀ [52]	×	M 6 ♂ [264]				Average No. Young.	Synchronous Broods, A Series.	Synchronous Broods, M Series.
$A M$ 1		6	42		79		42	43	273
$A M$ 2	167	♀ sterile	St.	St.	198	201	189	126	146

productiveness. Others are as productive as the uncrossed M or N races.

(6) It follows from the facts stated in 3–5 that a tendency to low productiveness and sterility on the part of the female may be transmitted through either sex as a racial character. When so transmitted it con-

TABLE XVI.

$A N$ SERIES.

(Cross 6, page 747; see also Table XVII.)

Generation.	A 36.17 ♀ [52]	×	N 5 ♂ [367]		Average No. Young.	Synchronous Broods, A Series.	Synchronous Broods, N Series.
$A N$ 1	11	55	114	55	59	43	302

forms imperfectly with Mendel's law of alternative inheritance. Fertility is commonly dominant over low productiveness, but not invariably. See Table XV, $A M$ 2, in which generation half the pairs are sterile. This case is exceptional. Low productiveness commonly skips a generation following a cross, but may be transmitted *directly* through the *female parent*. Its reappearance after skipping a generation is not certain. If selection is made from the most fertile cross-bred broods, low productive-

TABLE XVII.

GENEALOGY OF *AN* SERIES.

(Cross 6, page 747; see also Table XVI.)

$$A\ 38.3\,♀ \times N5\,♂$$
$$[145] \quad\longrightarrow\quad [367]$$
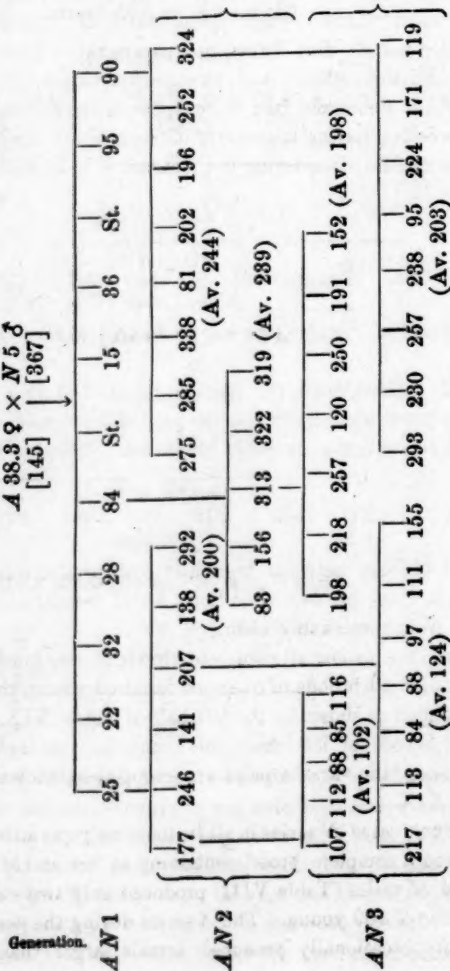
	Synchronous Broods, N Series.	Synchronous Broods, A Series.	Average No. Young.
	302	106	47
	308	128	229
	242	174	162

ness may not reappear in the following generation. Hence we can only say that low productiveness has a *tendency* to be inherited in alternative fashion, *skipping a generation*, but the alternative character of the inheritance is not sharp as is that of albinism and other typical Mendelian characters.

If low productiveness were a typical Mendelian recessive character, we should expect it regularly to reappear after skipping a generation, and to occur on the average in one fourth of the daughters produced by cross-bred pairs. But it does not always skip a generation. See Table XIX. Further, when it does, as expected, skip the first cross-bred generation (F_1) it sometimes fails to reappear in the following generation (F_2), cross-breeding having apparently obliterated the low productiveness.

Nevertheless, considering the fact that it is impossible to draw a sharp

TABLE XVIII.

A X Series.

(Cross 7, page 747.)

Generation.								Average No. Young.	Synchronous Broods, *A* Series.
			A 36.1 ♀ × Stock-jar ♂ [?] [?]						
A X 1			33	132	22			62	43
A X 2	211	262	318	263	308	290		275	126

line of division between high and low productiveness, the alternative inheritance of the two conditions found respectively in race *A* and in *M* or *N* is remarkably clear.

If we class as *low* all complete broods of one hundred young or fewer, and as *high* all broods of over one hundred young, then the various pairs are grouped as shown in the left half of Table XIX. But if we class as *low* all broods of less than 150 young, and as *high* all broods of over 150 young, the various pairs are grouped as shown in the right half of Table XIX.

The uncrossed *N* series in all its fourteen generations (Table IX) never produced a complete brood containing as few as 150 young, and the uncrossed *M* series (Table VIII) produced only two such broods, one of 67, the other of 109 young. The *A* series during the period under consideration only occasionally produced broods larger than 150. Accordingly

TABLE XIX.

NUMBERS OF PAIRS LOW OR HIGH, RESPECTIVELY, IN PRODUCTIVENESS,
AMONG THE CROSS-BREDS AND AMONG THEIR CHILDREN.

Among Cross-breds from Cross M or N ♀ × A ♂.	Broods under 100.	Broods over 100.	Broods under 150.	Broods over 150.
MA 2, Table X	0	7	0	7
" " XI	0	5	0	5
NA 2, " XIII	0	6	0	6
" " XIV	0	10	0	10
Totals	0	28 All high	0	28 All high
Among Cross-breds from Cross A ♀ × M or N ♂.				
AM 2, Table XV	3	3	3	3
AN 2, " XVII	2	17	4	15
AX 2, " XVIII	0	6	0	6
Totals	5 One in six low	26	7 One in four or five low	24
Among *Children* of Cross-breds from Cross M or N ♀ × A ♂.				
MA 3, Table X	4	7	6	5
" " "	0	12	0	12
" " XI	1	4	1	4
NA 3, " XII	7	8	9	6
" " XIII	0	8	0	3
" " XIV	0	8	0	8
" " "	0	8	1	7
Totals	12 One in five low	50	17 One in three or four low	45
Among *Children* of Cross-breds from Cross A ♀ × M or N ♂.				
AN 3, Table XVII	2	3	5	0
" " "	0	7	1	6
" " "	3	4	5	2
" " "	1	7	2	6
Totals	6 One in four or five low	21	18 One in two low	14

broods of fewer than 100 young are clearly like A broods, those of over 150 young are like M and N broods in size. Those between these limits might fall in either category, but would be more characteristic of the A series.

Among the 89 broods reared from the children of cross-breds, 18 (or 20.2 per cent) are under 100 in size, while 30 broods (or 33.7 per cent)

TABLE XX.

EFFECT OF SELECTING PAIRS FROM BROODS MORE OR LESS PRODUCTIVE BUT OF SIMILAR ANCESTRY.

Generation in which Selection was made.	Parental Broods.	Average Filial Brood.
MA 1, Table X	365	334
	379	373
MA 2, Table X	200	181
	229	294
AN 1, Table XVII	25	200
	84	239
	90	244
AN 2, Table XVII	177	102
	207	124
	313	198
	324	203

are under 150 in size. The expectation based on the hypothesis that low productiveness is a Mendelian recessive character is that 25 per cent of the broods will be low, which value lies between the two extremes named above, 20.2 per cent and 33.7 per cent.

Selection for High or Low Productiveness.

The inheritance of different degrees of fertility is unmistakable throughout these experiments and affords material for selection to act upon. Whenever pairs are taken simultaneously from broods of the same ances-

try but of different productiveness, the pairs taken from the more produc-
tive brood are invariably more productive, as a glance at Table XX will
show. If we weight alike each of the several cases included in Table
XX, we obtain the following average values from the *lower* and *higher*
broods respectively:

	Parental Brood.	Filial Brood.
Lower	196	197
Higher	232	239

We get here no evidence of regression. Compare page 741.

Is a Single Copulation sufficient to fertilize All the Eggs of a Female?

It is generally assumed that in many insects a single copulation (or
several within a brief period) suffices to fertilize all the eggs subsequently
produced by the female. That this is not so in Drosophila is indicated
by the following observations.

In generation *M* 13, Table II, a female was taken from a jar contain-
ing several males and put in a jar with food, where she laid eggs.
Pupae were removed from the jar as follows:

July	1	. . . . .	46
"	5	. . . . .	16
"	9	. . . . .	13
"	13	. . . . .	0
"	16	. . . . .	9
"	20	. . . . .	32
"	25	. . . . .	11 (Experiment closed.)

Fresh eggs were found in the jar July 9, and some of these were put
into a jar containing some fruit, but none of them hatched. The same
day a male was put in with the female, and, as shown above, the eggs
laid later were fertile. Likewise a cross-bred female which had been
with males for a few days was on June 12 put in a separate jar with
food. Pupae were found as follows:

June	26	. . . . .	21
July	1	. . . . .	21
"	5	. . . . .	0
"	9	. . . . .	0 (Male introduced.)
"	13	. . . . .	0
"	16	. . . . .	29
"	20	. . . . .	1

On July 9 a male was introduced, and pupae were again found after none had been found for over a week. These results show conclusively that a single copulation or several within a period of a few days is not necessarily sufficient to fertilize all the eggs in Drosophila.

ABSTRACT OF REPORT OF F. W. CARPENTER ON THE SIXTH INBRED GENERATION OF THE A SERIES.

To test the variability of the inbred flies, as compared with those not inbred, the following variable character was selected. On the proximal segment of the tarsus of the first pair of appendages there is present in the male a secondary sexual organ, comb-like in appearance, containing a variable number of chitinous teeth. This "sexual comb" has probably the function of a clasping organ in copulation. It is the number of teeth in this comb that has been taken as the variable character to be dealt with, the counting being done under the compound microscope.

The male Drosophila can often be distinguished with the unaided eye from the female by its smaller size and the darker color of the posterior segments of the abdomen. However, one can be quite certain of the sex only by examining the fly under the microscope, where the presence or absence of the sexual comb peculiar to the male can be noted.

In counting the teeth in the sexual comb the procedure was as follows: The sex of the preserved fly was determined under a low power of the microscope. If the fly proved to be a male it was removed from the stage of the microscope and the anterior pair of appendages was cut away from the body with a sharp scalpel. In order to do this more easily the head of the fly was first removed. The appendages were then examined under the high power of the microscope and the number of teeth in the sexual comb counted.

The Inbreeding Experiments.

The inbred material was obtained thus. A normal male and female were placed in a jar with food. The pair lived here, and from their off-spring several males and several females were selected. Of these, one male and one female were placed in each of several jars with food. Brothers and sisters were thus bred together. The most promising one of these latter cultures was selected to perpetuate the line and the other cultures were rejected. Certain of the offspring of this selected culture were treated in the way just described for their parents, and so the successive generations of inbred flies were obtained.

When the sixth inbred generation was reached, three cultures,

designated later as " Families A, B, and C," were carried through, each
having as parents a brother and sister belonging to the fifth genera-
tion.   All of the flies appearing in these cultures were preserved in 70
per cent alcohol, so that the whole number of offspring was obtained.
The parents were well supplied with food and kept until they died.   The
female parent of each culture was transferred at the end of about every
ten days to a new jar.   Imagoes began to appear in the first jar while
the female parent was still alive and laying eggs.

A control stock culture was maintained during the year under a large
bell-jar.   Here the flies were allowed to breed without interference.
They required no care except to be provided from time to time with
fresh food.

(a) *Effect on fertility and sexual proportion.*   In the three cultures
of the sixth generation designated " Families A, B, and C," all the off-
spring were saved.   The numbers of these and their sexual proportions
were as follows :

	A.	B.	C.
Males	46 (47.9%)	76 (50.3%)	64 (50.4%)
Females . . .	50	75	63
Totals . . .	96	151	127

No accurate determinations were made of the number of offspring of a
normal pair of flies, but from such observations as were made it is
probably safe to say that no striking falling off in fertility is to be seen
in the sixth inbred generation.   No indication of weakness was observed
among the flies.

Since the sexual proportion is near equality (possibly with a slight
excess of males), the figures given above indicate, on the whole, no
marked change in this respect.

(b) *Effect on variability.*   The number of teeth was counted in the
eighty sexual combs of forty males taken at random from the control
stock culture, and the results were plotted in the form of a frequency
polygon (Figure 5, N).   In addition the teeth were counted in the same
number of combs in the case of each of the inbred cultures, A, B, and
C.   These results were also plotted in frequency polygons (Figure 5,
A, B, C).

It will be seen that the number of teeth in the sexual comb is higher
in all the inbred families than in the normal flies (N) studied.   Both
means and modes are higher for the inbred flies.   But it is doubtful
whether this is the result of inbreeding, for the male employed in start-

ing the inbreeding experiment, the common ancestor of all the inbred families, had twelve teeth in his right comb, ten in the left, numbers higher than the normal and very similar to those prevailing among the inbred descendants of the male in question.

The variability in number of teeth has apparently been neither increased nor diminished by the inbreeding.[1]   The inbred flies have a slightly higher standard deviation, as we should expect from the fact
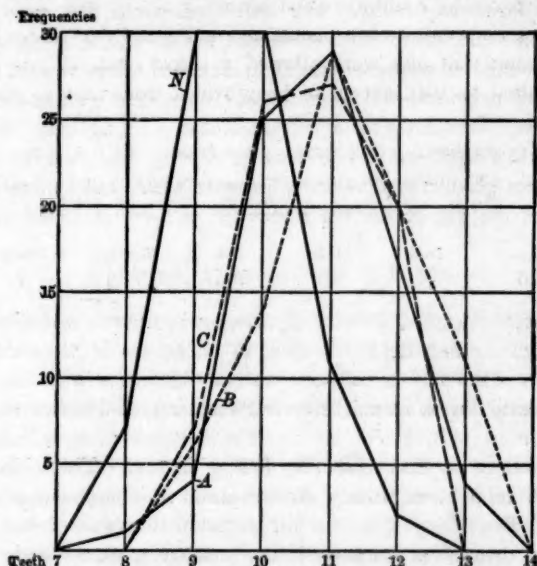
FIGURE 5. Variation in number of teeth on the sex-comb of forty males from each of three different broods (A, B, and C) of a stock inbred for six generations, and of males (N) from a stock not inbred.

that they have higher means, but the coefficient of variability (ratio of standard deviation to mean) is in family B a little greater than in the normal flies, while in families A and C it is a little less.

The number of teeth is about the same, and varies in a similar way on the two sides of the body, as is shown by plotting separately the numbers

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[1] An examination was subsequently made by A. H. Clark of the variability of the sexual comb in 45 males of the *fifteenth* inbred generation.   This was found to be almost identical in character with what it had been in the sixth generation. The range of variation was still from 8 to 13, with the mode at 11, the mean at 10.79.

for each side. The degree of correlation between the numbers on the two sides of the body is very small. This means that the right and left legs are to a great extent independently variable in number of teeth, which would lead one to suppose the variability dependent largely upon local conditions within the pupa.

Influence of Light of Different Colors.

(a) *Influence on fertility.* For about ten weeks flies were allowed to breed in chambers so constructed that the only light admitted passed through colored solutions contained in flattened glass vessels. These colors were red, blue, and green. An orange chamber was also in use, but its culture died out after about six weeks. In addition, flies were bred in white light and in darkness.

Below are given the numbers of imagoes which had appeared in the cultures at the end of the ten weeks:

White.	Dark.	Blue.	Red.	Green.	Orange.
93	67	68	104	73	?

These numbers are of doubtful significance because of several unknown factors entering into the result, such as differences in vigor among the progenitors of the various cultures, possible differences in quality of food, etc. The experiment should be several times repeated before conclusions are drawn.

(b) *Influence on phototropic responses of larvae.* The older larvae were observed to be negatively phototropic in their responses to ordinary daylight. In seeking situations for pupation they were found to have distributed themselves as follows in the rectangular glass vessels in which they were contained in the various chambers. The distribution was determined by the position of the pupa cases.

	White.			Blue.			Red.			Green.			Orange.		
	Front.*	Back.*	Sides.	Front.	Back.	Sides.	Front.	Back.	Sides.	Front.	Back.	Sides.	Front.	Back.	Sides.
	9	29	10	15	68	40	21	64	34	18	36	36	8	26	23
Percentage at back	60%			55%			54%			40%			45%		

* "Front" indicates side of vessel toward light, "back," side away from light.

The considerable proportion of individuals which pupated on the front side of the several chambers is doubtless made up largely of individuals which pupated at night, when the directive effect of light would be eliminated, or nearly so. White light evidently has the strongest directive effect, while blue and red are about equally effective, orange and green being less effective still. The observed effects are perhaps due to differences in the intensity rather than in the quality of the illumination in the various chambers.

It is probable that the larvae avoid light of *every* kind at pupation, for in each of the five cultures more pupae are found on the back of the chamber than on its front. No emphasis is laid on the qualitative result obtained because the lights employed were not entirely pure and the intensities were not uniform, so that from this experiment alone it is impossible to say whether or not any one sort of ray is more influential than another in determining the result.

Age at which Sexual Maturity is attained.

Certain experiments were made to determine the earliest time after emergence of the imagoes at which fruitful matings could occur between the sexes. In four cases males and females were left together for twenty-four hours or less, after hatching, and then separated. None of these females laid fertile eggs. Two females which were left with males for thirty-nine hours after hatching and then separated both laid fertile eggs. It follows that the flies become sexually mature at some time between twenty-four and thirty-nine hours after hatching. The time was not more precisely determined.

Is a Male capable of Copulating more than Once?

Yes, as the following experiment shows.

Four unfertilized females were placed in a jar with a single male, which had not yet copulated, and left for twenty-seven hours. Each female was then placed in a separate jar and the male allowed to escape. All the females produced offspring.

As a control on this experiment, two virgin females were placed in a jar with food. After a few days several eggs were observed, but none of these hatched. [This experiment has since been several times repeated, always with the same result. Apparently Drosophila is incapable of parthenogenetic reproduction. W. E. C.]

Studies by W. M. Barrows of Variation in Number of Teeth
on Male Sex-Comb, and of Variation in Size.

To determine whether long-continued inbreeding had affected the
variability of the character, number of teeth on sex-comb of male, Mr.
Barrows has examined individuals from three different inbred series, *A*,
M, and *N*, and from one stock not inbred, *X*. These experiments show

TABLE XXI.

Correlation in Number of Spines between Sex-combs of Right and
Left Legs, Sixth Inbred Generation, *A* Series.

Left leg (*x*).

	Spines	9	10	11	12	13	Sums
	8	..	1	..	..	..	1
	9	..	4	1	..	1	6
Right leg (*y*).	10	3	7	6	10	2	28
	11	6	18	17	11	6	58
	12	2	11	8	6	1	28
	13	..	1	..	2	1	4
	Sums	11	37	32	29	11	120

Mean number of spines, left leg $= A\,x = 10.93$
"   "   "   right leg $= A\,y = 10.94$
Standard deviation   .   left leg $= \sigma x = 1.453$
"   "   "   .   right leg $= \sigma y = 1.230$
Coefficient of correlation . . . . $r = .022 \pm .061$

no appreciable effect of inbreeding. In every case the brood reared
under the best and the most uniform conditions has the highest average
number of teeth, irrespective of whether or not it is inbred. The same
may be said of variation in size. Inbreeding has diminished neither the
average size nor the variability in size.

The series and generations studied were *A* 61, *M* 31, *N* 30, and *X* 1.
The origin and history of the first three has been described in detail in
the earlier parts of this paper. Series *X* originated from two pairs of
flies caught in Cambridge in October, 1905. Series *N* died out for lack

of food in the thirtieth generation, and the measurements were made from dry dead flies found in the bottom of the jar. This culture shows a unique variability.   Series *A, M,* and *X* were breeding under the same good conditions and side by side when the specimens were taken for special study.

Out of the preserved material of each of the four series one hundred

TABLE XXII.

CORRELATION IN NUMBER OF SPINES BETWEEN SEX-COMBS OF RIGHT AND LEFT LEGS, SERIES *A*, GENERATION 61.

Left leg (*x*).

	Spines	8	9	10	11	12	13	14	Sums
	7	..	1	..	..	..	..	..	1
	8	1	1	1	..	..	..	..	3
Right leg (*y*).	9	..	2	9	2	1	..	..	14
	10	..	6	10	8	3	..	..	27
	11	1	4	10	18	6	1	1	41
	12	..	..	1	4	6	..	..	11
	13	..	..	..	1	1	..	..	2
	14	..	..	..	..	1	..	..	1
	Sums	2	14	31	33	18	1	1	100

$$A\,x = 10.58 \qquad \sigma\,x = 1.087$$
$$A\,y = 10.50 \qquad \sigma\,y = 1.136$$
$$r = 0.469 \pm .05261$$

males were selected at random, the measurements being made as follows:

The fly was held on its back, under a dissecting microscope, by needle points, and the right and left fore legs of the fly were then pulled off and laid on a glass slide.   Next, the right hind leg was pulled off, and also laid on the slide.   These parts were then covered with a cover glass, and examined under a compound microscope.   The number of spines in each sex-comb was counted and recorded.   The length of the tibia of the hind leg was ascertained by means of an ocular micrometer, the record

being made in divisions of its scale, one division of which was equal to 0.017 mm.

From the data thus gathered were constructed Figures 6 and 7 and Tables XXII–XXVII. Table XXI is based on observations made by F. W. Carpenter (see page 773). He counted the spines on the sex-combs of both fore legs of forty males from each of three jars, *A*, *B*, and *C* of the sixth inbred generation of the *A* series, and also of forty males from a stock culture considered " normal." The variation in number of
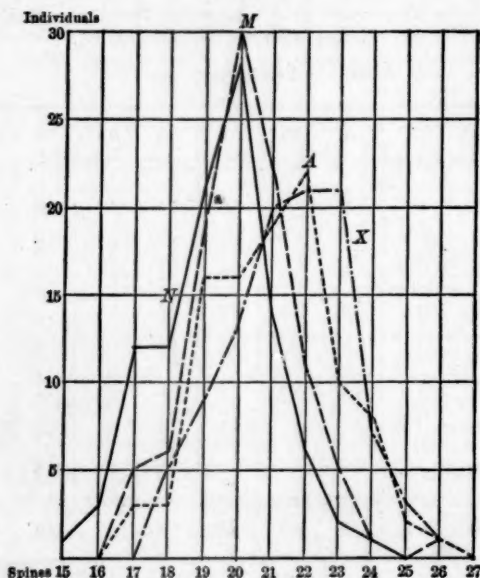

FIGURE 6. Variation in number of spines on the two sex-combs of one hundred males from each of four different series; *A*, from generation *A* 61; *M*, from *M* 31; *N*, from *N* 30; and *X*, from *X* 1.

spines in each of these four lots is shown in Figure 5, and for the three inbred lots combined in Table XXI. That table shows also the degree of correlation in number of spines which exists between the two sides of the body in the sixth inbred generation of the *A* series. The same thing is shown for the sixty-first generation of the *A* series in Table XXII, and for the first inbred generation of the *X* series in Table XXIII. A comparison of these three tables indicates that the correlation between right and left sides is probably not increased by inbreeding, for though

the correlation is greater in A 61 than in A 6, it is not materially greater in the former than in the not-inbred X series. The close resemblance between A 61 and X 1 is probably due to the fact that they were reared under similar conditions.

In Table XXVIII are brought together for comparison constants derived from the several correlation tables, XXI–XXVII. From a
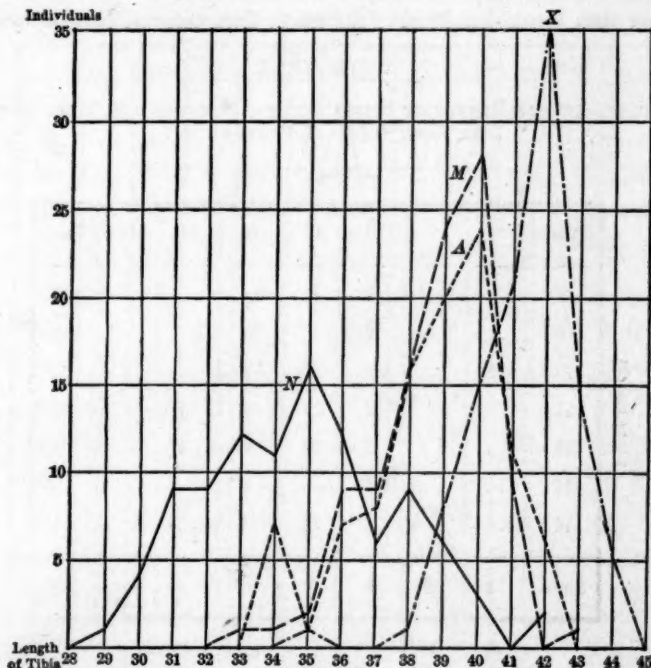
FIGURE 7. Variation in length of tibia of one hundred males from each of four different series; A, from generation A 61; M, from M 31; N, from N 30; and X, from X 1.

study of this we learn the close dependence of the variability of Drosophila upon external conditions. Compared with these factors inbreeding is of little consequence.

The well-nourished cultures (A 61, M 31, and X 1, Figures 6 and 7) show a higher mean number of spines and a greater tibial length than cultures reared under poor or variable conditions of nutrition, such as

N 30 (Figures 6 and 7) and Carpenter's "normal" individuals (Figure 5, N). This is true irrespective of the inbredness of the different cultures. This conclusion is supported by a comparison of the A series in the sixth inbred generation (A 6, B 6, and C 6) and in the sixty-first generation (A 61). Conditions were optimum in both cases; the average number of spines and the variability are similar. Contrary to the common opinion, the variability would seem to have been increased rather than diminished by the inbreeding, since the coefficient of varia-

TABLE XXIII.

CORRELATION IN NUMBER OF SPINES BETWEEN SEX-COMBS OF RIGHT AND LEFT LEGS, SERIES X, GENERATION 1.

Left leg (x).

	Spines	8	9	10	11	12	13	14	Sums
Right leg (y).	8	..	..	1	1	1	..	..	3
	9	..	3	5	..	1	..	..	9
	10	1	3	9	8	4	..	..	25
	11	..	3	11	14	6	1	..	35
	12	..	..	3	14	6	1	..	24
	13	..	..	1	..	2	..	..	3
	14	..	..	..	..	1	..	..	1
	Sums	1	9	30	37	21	2		100

$$A\,x = 10.74 \qquad \sigma x = 1.094$$
$$A\,y = 10.81 \qquad \sigma y = 1.186$$
$$r = 0.301 \pm .06133$$

tion is greater for the sixty-first than for the sixth inbred generation; but this difference may be due to the small numbers of individuals examined, particularly in the cultures of the sixth generation, each of which furnished only forty males.

The measurement, tibial length, is probably a good index of relative size of the individuals in the cultures measured. If so, we may infer that the individuals of X 1 are larger than those of the other three cultures measured, which fact would indicate that inbreeding tends to

diminish size. Yet the effect of this factor is small as compared with the effects of nutrition, for N 30 and M 31 differ in tibial length by four units, though inbred practically the same amount; but M was reared

TABLE XXIV.

CORRELATION BETWEEN NUMBER OF SPINES IN SEX-COMBS AND LENGTH OF TIBIA, SERIES N, GENERATION 30.

x = spines (sum of both legs).

y = length of tibia.	15	16	17	18	19	20	21	22	23	24	Sums
29	..	..	1	..	..	..	..	..	..	..	1
30	..	..	2	2	..	..	..	..	..	..	4
31	1	1	3	2	1	1	..	..	..	..	9
32	..	..	3	1	4	1	..	..	..	..	9
33	..	1	2	2	4	3	..	..	..	..	12
34	..	1	..	3	3	4	..	..	..	..	11
35	..	..	..	2	3	10	1	..	..	..	16
36	..	..	1	..	2	5	4	..	..	..	12
37	..	..	..	..	3	..	..	1	2	..	6
38	..	..	..	..	..	3	3	2	..	1	9
39	..	..	..	..	1	..	3	2	..	..	3
40	..	..	..	..	..	1	2	..	..	..	3
41	..	..	..	..	..	..	..	..	..	..	0
42	..	..	..	..	..	..	1	1	..	..	2
Sums	1	3	12	12	21	28	14	6	2	1	100

$$A x = 19.38, \quad \frac{A}{2} = 9.69 \qquad \sigma x = 1.684$$
$$A y = 34.80 \qquad\qquad\qquad \sigma y = 2.842$$
$$r = .7075 \pm .0337$$

under uniformly good conditions, N under varying conditions, which finally became intolerable. Again M 31 and A 61, which differ by thirty generations in inbredness, but were reared under identical conditions, have an almost identical tibial length. This is exceeded, however, by

three units in the X 1 culture, which was not inbred beyond a single generation. This difference probably represents, in part at least, an effect of inbreeding, which shows itself between the sixth and the thirty-first generations. Compare the variation in spines of X 1, A 6–C 6, M 31, and A 61, all of which were reared under optimum conditions. Number of spines is correlated with tibial length, as we shall see, and

TABLE XXV.

CORRELATION BETWEEN NUMBER OF SPINES IN SEX-COMBS AND LENGTH OF TIBIA, SERIES A, GENERATION 61.

x = spines (sum of both legs).

	17	18	19	20	21	22	23	24	25	26	Sums
34	3	..	2	..	..	2	..	..	..	..	7
35	..	..	..	..	..	1	..	..	..	..	1
36	..	1	1	2	2	1	..	..	..	..	7
37	..	1	2	3	1	1	..	..	..	..	8
38	..	1	5	3	..	6	..	1	..	..	16
39	..	..	5	3	7	1	1	2	..	1	20
40	..	..	1	2	6	4	5	4	2	..	24
41	..	..	..	2	3	4	1	1	..	..	11
42	..	..	..	1	..	2	3	..	..	..	6
Sums	3	3	16	16	19	22	10	8	2	1	100

(y = length of tibia.)

$$\frac{A x}{2} = 10.55 \qquad \sigma x = 1.8574$$
$$A y = 38.72 \qquad \sigma y = 2.031$$
$$r = .4687 \pm .0526$$

the number of spines in A 6–C 6 was slightly higher than in A 61. It is fair to suppose that the tibial length also was slightly greater, and so the size. These differences may have been due simply to differences in nutrition, but the fact that X 1, which was reared under the same conditions as A 61, yet exceeds it in number of spines and tibial length, suggests that A 6 may exceed A 61 for the same reason, that is, because less inbred.

The correlation between number of spines and length of tibia is considerable. It increases as the variation in tibial length increases, being over .70 in N 30, in which lot the greatest diversity of tibial lengths occurred; in its production occurred the greatest variations in food supply. The variation in number of spines increases in nearly the same

TABLE XXVI.

CORRELATION BETWEEN NUMBER OF SPINES IN SEX-COMBS AND LENGTH OF TIBIA, SERIES M, GENERATION 31.

$x =$ spines (sum of both legs).

$y =$ length of tibia.	17	18	19	20	21	22	23	24	25	26	Sums
33	..	1	..	..	..	..	..	..	..	..	1
34	..	..	1	..	..	..	..	..	..	..	1
35	..	1	1	..	..	..	..	..	..	..	2
36	..	1	4	3	1	..	..	..	..	..	9
37	1	2	2	1	3	..	..	..	..	..	9
38	1	..	3	9	3	..	..	..	..	..	16
39	2	1	5	6	7	3	..	..	..	..	24
40	1	..	3	6	5	8	4	1	..	..	28
41	..	..	..	4	3	..	1	..	..	1	9
42	..	..	..	..	..	..	..	..	..	..	0
43	..	..	..	1	..	..	..	..	..	..	1
Sums	5	6	19	30	22	11	5	1	0	1	100

$$\tfrac{1}{4} A x = 10.115 \qquad \sigma x = 1.568$$
$$A y = 38.70 \qquad \sigma y = 1.723$$
$$r = .4476 \pm .0539$$

order as the tibial lengths, among the several lots, so that it is clear that substantially the same factors govern both, the correlation between the two becoming more pronounced as the variability becomes greater. This variability is dependent largely upon temperature and food supply, inbreeding being a factor entirely negligible.

TABLE XXVII.

CORRELATION BETWEEN NUMBER OF SPINES IN SEX-COMBS AND LENGTH
OF TIBIA, SERIES X, GENERATION 1.

x = spines (sum of both legs).

	18	19	20	21	22	23	24	25	26	Sums
35	..	..	..	..	..	1	..	..	..	1
36	..	..	..	..	..	..	..	..	..	0
37	..	..	..	..	..	..	..	..	..	0
38	..	1	..	..	..	..	..	..	..	1
39	1	1	1	2	2	1	..	..	..	8
40	1	3	2	2	1	4	..	2	..	15
41	2	1	2	5	4	4	2	..	1	21
42	1	3	6	7	8	6	4	..	..	35
43	..	..	2	3	4	3	1	1	..	14
44	..	..	..	1	2	2	..	..	..	5
Sums	5	9	13	20	21	21	7	3	1	**100**

y = length of tibia.

$$\tfrac{1}{4} A x = 10.775 \qquad \sigma x = 1.7485$$
$$A y = 41.38 \qquad \sigma y = 1.461$$
$$r = .1413 \pm .066$$

SUMMARY.

1. Inbreeding probably reduces very slightly the productiveness of *Drosophila*, but the productiveness may be fully maintained under constant inbreeding (brother with sister) if selection is made from the more productive families.

2. In crosses of a race of low productiveness and inclined to sterility (race A) with a race of high productiveness (B) it has been found that a female of race A does not have her fecundity increased by mating with a male of race B, and conversely, a female of race B does not have her fecundity diminished by a mating with a male of race A. Hence every male not actually sterile furnishes an abundance of functional spermatozoa.

TABLE XXVIII

Constants derived from Tables XXI-XXVII brought together for Comparison.

Series and Inbred Generation.	Mean of Spines (A).	½ A Spines.	Mean of Spines, Right.	Mean of Spines, Left.	Standard Deviation, σ Spines.	Coeff't of Variation, Spines = σ/A.	Mode of Spines.	Mean Length of Tibia.	Standard Deviation of Tibia (σ).	Correlation (r) Spines and Tibia.
"Normal" (Carpenter)	19.28	9.64 ± .145	9.625	9.650	1.864 ± .1029	14.15	9 and 10	...	...	...
A 6	21.71	10.86 ± .1802	10.87	10.85	1.600 ± .1275	15.56	11	...	...	...
B 6	22.40	11.20 ± .1781	11.125	11.275	1.670 ± .1259	14.91	11	...	...	...
C 6	21.50	10.75 ± .1192	10.825	10.675	1.118 ± .0843	10.40	11	...	...	...
A 61	21.10	10.55 ± .1252	10.50	10.58	1.8574 ± .0885	17.60	11	38.72	2.031 ± .0969	.4887 ± .05261
X 1	21.65	10.775 ± .1179	10.81	10.74	1.7485 ± .0833	16.28	11	41.88	1.461 ± .0097	.1418 ± .006
M 31	20.23	10.115 ± .1058	10.11	10.11	1.568 ± .0748	15.51	10	38.70	1.723 ± .0821	.4476 ± .0589
N 30	19.38	9.69 ± .1186	9.75	9.63	1.684 ± .0795	17.38	9 and 10	34.8	2.842 ± .1355	.7075 ± .0387

3. The cross-breds produced by the mating, $B \; \female \times A \; \male$, are all of high productiveness.

4. The cross-breds produced by a mating $A \; \female \times B \; \male$ are usually, but not always, of high productiveness.

5. The children of both sorts of cross-breds (see 3 and 4) are some of high productiveness like race B, others of low productiveness, like race A.

6. Low productiveness is inherited after the manner of a Mendelian recessive character in certain of the crosses made, skipping a generation and then reappearing. In other cases it has failed to reappear in generation F_2, indicating its complete extinction by the cross. In a few cases it has failed to be dominated by high productiveness in generation F_1. In such cases the female parent has always been of race A. Hence low productiveness (or sterility) of the female may be transmitted directly through the egg from mother to daughter, but only indirectly through the sperm, the character skipping a generation.

7. A cross between two races, one inbred for thirty or more generations and of low productiveness, the other inbred for less than ten generations and of high productiveness, produced offspring like the latter in productiveness, but not superior to it.

8. The same two races crossed after an additional year of inbreeding (about twenty generations) produced offspring superior to either pure race in productiveness.

9. Inbreeding does not affect the variability in number of teeth on the sex-comb of the male, nor the variability in size.

10. Size of the male individual is closely correlated with number of teeth in the male sex-comb.

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